Different mechanisms of goose influence both accelerate and retard the decomposition process in an Arctic wetland

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Paper 2

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Manuscript

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ABSTRACT

Background and aims Due to human induced changes in their wintering grounds, goose numbers increased dramatically over the past 50 years. To understand the consequences of these changes, studies on key ecosystem processes, like decomposition, on the breeding grounds in the generally severely nutrient limited Arctic are indispensable. This article reports on the influence of Barnacle Geese *Branta leucopsis* on the decomposition process and the release of nitrogen from litter on high-Arctic Svalbard (78° 55' N, 11° 56' E).

Methods The study made use of paired long-term exclosures and control plots. Litter and goose droppings were collected and subsequently analysed on chemical parameters to understand the influence of grazing via a change in dead organic matter quality within and between plant growth forms and faeces. Reciprocal transplantation of dead organic matter (graminoids, mosses, roots and faeces) between ungrazed (exclosures) and heavily grazed areas, using the litterbag technique, was used to study the goose grazing influence on litter decomposition and nitrogen release through a shift in environmental conditions. The possibly facilitating role of goose faeces was investigated by studying decomposition in separate subplots with faeces addition in some of the exclosures.

Results In the exclosures almost twice the necromass of grazed plots was present and the contribution of litter originating from graminoids and roots was respectively twice and four times as much in the exclosures compared to the grazed plots. This is important seen the fact that these growth forms were found to differ in litter quality. Together with the place of production and thus incubation, this resulted in a decrease in decomposition and nitrogen release rates in the following order: roots, graminoids and moss. Goose-induced changes in litter composition thus impeded decomposition. Environmental impact of geese, in contrast, was found to enhance decomposition, but not nitrogen release rates of the same litter type. Goose faeces, characterised by a distinct chemical quality, were found to decompose as slow as moss litter and release nitrogen as fast as graminoid litter.

Keywords: *litter quality, faeces, roots, nitrogen, decomposition, herbivory, goose, Arctic*

INTRODUCTION

Given their importance for ecosystem functioning and their possible influence on climate change, decomposition processes have been intensively studied with regard to global change. Mostly, these studies focused on the climate effects on decomposition (Aerts 1997, Cornelissen et al. 2007). However, global change encompasses much more. Examples of other well documented global changes are: alterations in the biogeochemistry of the global nitrogen cycle, on-going land use / land cover change (Vitousek et al. 1994) and an altered distribution and abundance of much of Earth's biota (Wardle and Bardgett 2004). The increased population numbers of the Western Palearctic Arctic breeding geese in the last 50 years (Madsen et al. 1996, O'Connell et al. 2006) are an example of the latter. Recent changes in climate, land use and the implementation of protective measures (e.g. reduced hunting pressure and improved refuge areas) have dramatically improved the birds' ability to survive the winter (van Eerden et al. 1996, Fox et al. 2005, Gauthier et al. 2005, Kéry et al. 2006), resulting in an increased grazing pressure both in the temperate wintering areas and in the higher latitude breeding sites of these migratory herbivores.

While the increase in goose numbers is primarily due to changes in the temperate wintering areas, the changes in decomposition processes due to grazing are likely to be of key importance in systems where low temperature and poor drainage result in low nutrient availability (Nadelhoffer et al. 1992). An example of such area is Svalbard's tundra, where the once endangered Svalbard Barnacle Geese *Branta leucopsis* (Bechstein, 1803) increased by two orders of magnitude over the past 60 years (from 300 birds in 1948 to almost 28 000 birds in 2006; Pettifor et al. 1998, O'Connell et al. 2006).

Grazing by geese and other herbivores strongly affects tundra systems (Cooch et al. 1991, Jano et al. 1998, Gornall et al. 2009). A major challenge in understanding herbivory effects on ecosystem functioning is to understand the linkages between above-ground and below-ground components in natural communities. In particular litter decomposition, a major factor for nutrient cycling and a strong determinant of the CO_2-fluxes from the soil to the atmosphere (Aerts 1997), is a key process that is likely influenced by (changes in) goose grazing. However despite the increased recognition of the importance of grazer effects on litter decomposition (Frank and Groffman 1998, Stark et al. 2000, Olofsson et al. 2001), our knowledge of how goose grazing influences decomposition is still limited.

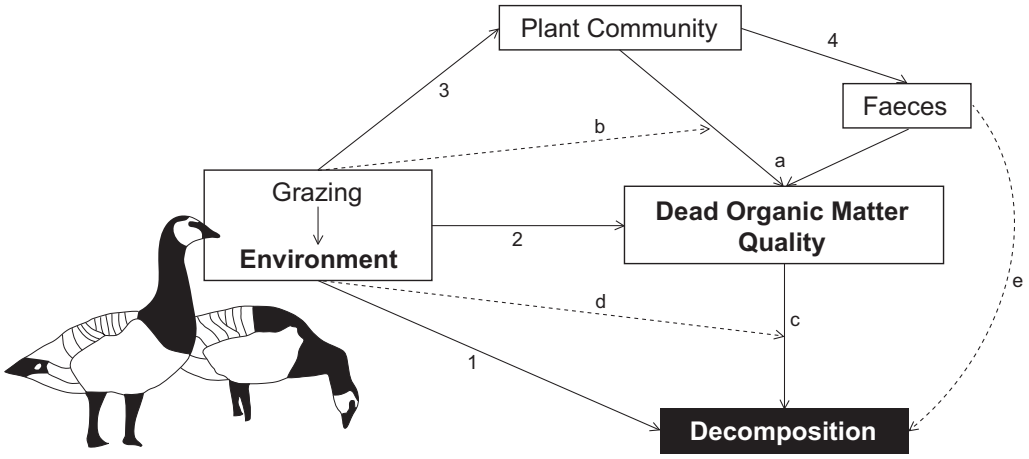

Figure 2.1. Simplified schematic representation of the ways in which goose grazing may affect decomposition i.e. through changes in the environmental conditions for decomposition (1) and more indirectly through changes in the quality of dead organic matter (2) which may be caused by shifts in community composition (3) and the production of faeces (4). Feedback mechanisms are not included. The first section of this paper focuses on dead organic matter quality. We investigated whether goose grazing affects the litter abundance of four common wetland growth forms (non-sphagnum mosses, monocotyledons, dicotyledons and equisetales) and roots (3), if growth forms and faeces differ in dead organic matter quality (a), whether goose grazing influences litter quality within growth forms (b). The second section focuses on the decomposability and nitrogen release rates. We investigated whether the dead organic matter produced in grazed plots differed in decomposability and nitrogen release rates compared to dead organic matter produced in exclosures (c), whether goose grazing influences decomposability and nitrogen release from identical dead organic matter (1) and if this alters the pattern observed for c (d). Finally we studied if faeces might stimulate decomposition and nitrogen release from organic matter (e). Answers to these questions are important if we are to understand potential effects of geese on the ecosystem level processes decomposition and nutrient availability. (Adapted from Dorrepaal et al. 2005)

Controls of litter decomposition include dead organic matter quality (figure 2.1, 2, Swift et al. 1979, Hobbie 1996, Lang et al. 2009) and environmental conditions (figure 2.1, 1, Vitousek et al. 1994, Aerts 1997, Berg and McClaugherty 2008), including the decomposer community (Swift et al. 1979, Ayres et al. 2009). Geese might interact with each of them (figure 2.1).

Selective grazing (Black et al. 2007) and the alteration of environmental conditions such as soil temperature following goose grazing (van der Wal et al. 2001), can alter vegetation composition (figure 2.1, 3). Indeed, goose grazing was found to be able to impact severely on the vegetation composition in a range of Arctic habitats (Bazely and Jefferies 1986, Gauthier et al. 2004) and also the Barnacle Goose population on Svalbard seems to induce a shift in both distribution of plant growth forms and species within growth forms (paper 1, Loonen and Solheim 1998, van der Wal et al. 2001, Stech 2008, Kuijper et al. 2009). Previous studies

revealed that especially a shift in plant growth form composition can largely influence litter decomposition via a change in litter quality (figure 2.1, a, Cornelissen et al. 2007).

However, resource quality for decomposition is also influenced through grazing-induced changes in litter quality within species/growth forms (figure 2.1, 2, Kielland et al. 1997, Olofsson and Oksanen 2002), and responses might be species/growth form specific. Finally, (goose) herbivory transforms plant tissues into faeces (figure 2.1, 4), which tends to release nitrogen faster than plant litter (Bazely and Jefferies 1985), thus providing an important shortcut for nutrient cycling in the Arctic tundra where production and biomass accumulation are strongly nutrient limited (Shaver and Chapin 1986, Shaver and Chapin 1995, Jonasson et al. 1996). Moreover, the addition of nitrogen from faeces might stimulate the microbial activity (Bazely and Jefferies 1985) and thus enhance decomposition and nitrogen release from organic matter (figure 2.1, e).

Whereas goose grazing affects the decomposition process more indirectly by changing the resource quality, the goose-induced changes in the environment might also more directly impact decomposition and nutrient release rates (figure 2.1, 1). Indeed other authors observed an impact of geese on soil temperature (van der Wal et al. 2001) and moisture through a reduction in the insulating moss layer and nutrient availability (Wilson and Jefferies 1996, Gornall et al. 2009), three environmental factors which are directly related to the rate of the decomposition process (Robinson et al. 1995, Hobbie 1996, Aerts et al. 2006).

Moreover geese influence the microbial communities (paper 1), which are involved in the decomposition process. If the different soil communities are specialized in decomposing the litter produced above them, a so-called 'home-field advantage' might arise (Ayres et al. 2009); meaning that leaf litter decomposes more rapidly beneath the plant species it is derived from, than it does beneath different plant species (figure 2.1, d) (Bocock et al. 1960, Vivanco and Austin 2008). So found Olofsson and Oksanen (2002) for their study on reindeer grazing that shrub litter decomposed faster in the lightly grazed area where shrubs were common, and graminoid litter decomposed faster in the heavily grazed area where graminoids were common.

The objective of this study is to investigate following potential ways of Barnacle Goose impact on decomposition and nitrogen release rates:

- Goose-induced shifts in the quality of dead organic matter (figure 2.1, a, b)
- Goose-induced changes in the abiotic and biotic environment (figure 2.1, c, d)
- A facilitation effect of goose faeces (figure 2.1, e)

MATERIAL AND METHODS

Study site

The study was carried out in the Kongsfjorden area (78.55°N, 11.56°E) at Spitsbergen, Svalbard. The growing season is short with snowmelt around the beginning of June, followed by the thaw of the active layer covering the permafrost. The active layer gradually increases in depth until the end of August and the first new snow arrives around the start of September. Mean annual precipitation is 370 mm, which falls mostly outside the growing season, and mean annual temperature is -4.4 °C (data from www.eKlima.no, delivered by the Norwegian Meteorological Institute). In 1980, a first couple of breeding Barnacle Geese was observed in the area (Tombre et al. 1998). Over the subsequent years the new established population grew until a high of 900 adults in 1999 to fall back and stabilize between 450 and 800 adults (Kuijper et al. 2009). Barnacle Geese breed mainly on the islands in the fjord (Tombre et al. 1998). After hatching, during chick rearing and moulting, the area in and around Ny-Ålesund, our study site, is intensively used as forage habitat by families and non-breeders alike (Loonen et al. 1998). The depth of the soil organic layer is variable and exists mainly of poorly decomposed moss litter. The vegetation of this wetland is characterized by a continuous mat of mosses (*Calliergon* spec. as the most abundant) (Kuijper et al. 2009). *Arctodupontia scleroclada* (Ruprecht) Tzvelev dominates the vascular plant composition. Grazing impact by other herbivores than Barnacle Geese is negligible. Just a few Pink-footed Geese *Anser brachyrhynchus* (Baillon, 1834) were observed for a short time at beginning of the season and although reindeer *Rangifer tarandus platyrhynchus* (Linnaeus, 1758) are observed throughout the season, grazing pressure by them is considered to be low (Kuijper et al. 2009).

Experimental design

To address the research questions we made use of paired grazed and ungrazed plots. For the ungrazed plots grazing was prevented by exclosures, which were made of chicken-wire 0.5 m high. Exclosures were erected on different times and in different habitats in the close neighbourhood of Ny Ålesund. The longest distance between two exclosures was 670 m. Exclosures were divided in three series. The first series, further named 'Solvatnet' was erected in 1998 and exists of five exclosures (0.8 m x 0.8 m) around the lake Solvatnet. The exclosures were characterised by dry (1), moist (2) and wet (2) vegetation. All were dominated by mosses. An area within 1 m distance from the exclosures with vegetation characterized by natural grazing was used as the reference paired grazed plot. The second series, further named 'Thiisbukta' exists of six exclosures (2 m x 2 m) erected in 2003 along a moisture gradient in the Thiisbukta wetland. At the same time an identical reference plot was defined for each exclosure in the close neighbourhood. The exclosures of both the Solvatnet and Thiisbukta series were protected with a cross of wires on top in order to prevent geese from landing in the exclosures. The 'old series' finally forms a third and more heterogeneous group which exists of older (two from 1991 and one from 1992, 1993 and 1994 each) exclosures of different sizes (between 0.5 m x 0.5 m and 1 m x 1 m) spread all over the village. As these exclosures lacked a proper reference plot, they were randomly assigned one in the close vicinity of the exclosure.

Relative abundance of different litter types

The relative abundance of different litter types was studied in grazed plots and exclosures of the Thiisbukta series at the end of the growing season in 2007. In each plot a pooled sample of four turfs (3 cm by 3 cm and 15 cm deep from the moss-soil surface, the limit for almost all roots) was taken. In the laboratory different litter types were carefully sorted out. Four categories were distinguished: moss litter (the brown photosynthetically inactive part of the moss layer which is still structurally intact), graminoid litter, dicotyledonous litter and roots (both bio- and necromass). A fifth category, *Equisetum* spec. litter, was expected but not found in the quantity samples. Litter was carefully cleaned, dried until constant weight at 35°C for at least 96 hours and weighted.

Quality analysis of litter

In autumn 2007 we also collected litter for quality analysis and the determination of decomposition and nitrogen release rates in both the exclosures and their control plots of all exclosure series. For the moss litter and roots, four turfs (5 cm by 5 cm and 15 cm deep) per plot were collected and sorted. Roots of all plants both dead and living were used. For the graminoids senescenced leaves, which were still attached to the plants were picked. No litter of dicotyledons or *Equisetum* spec. was collected as those litters were almost absent in the control plots and present only in very small amounts in the exclosures. Fresh goose faeces were collected around lake Solvatnet and in the Thiisbukta wetland and pooled in the end. All litter and faeces were air dried. Of each litter sample, a subsample was weighted, dried at 70°C until constant weight and reweighted to make the relation between air-dry and oven-dry mass and thus to calculate the initial oven-dry mass in each litterbag.

Table 2.1. Parameters and methods included in the Plant Quality Minimum Dataset from Palm and Rowland (1997) and used to characterize dead organic matter quality for decomposition +, -, * Indicates if the parameter is considered important for the process: (+) accelerating, (-) inhibiting or (*) important but depending on other factors (Melillo et al. 1989, Palm and Rowland 1997, Berg and McClaugherty 2008)

Parameters		**Methods**	**Short-term decomposition / Nutrient leaching**	**Long-term decomposition / SOM formation**
Carbon quality	'lignin'	ADF-H_2SO_4 (Van Soest 1963, Rowland and Roberts 1994)	-	-
	Soluble carbon	Aqueous methanol (50%) extraction followed by weight loss or simple sugars (Dubois et al. 1956, Allen 1989)	+	
	Soluble phenolics	Aqueous methanol (50%) extraction followed by Folin-Ciolcalteu assay (Constantinides and Fownes 1994a, b)	- (N-mineralization)	?
	α-Cellulose	ADF-residu (Van Soest 1963, Rowland and Roberts 1994)		*
Nutrient quality	Total nitrogen	CN element analysis (CN element analyser NC-2100, Carlo Erba Instruments, Italy)	+	+
	Total carbon	CN element analysis		
	Total Phosphorus	Kjeldahl (Anderson and Ingram 1993)	+	
	Ash-free dry weight	Ash for 3h 500°C	*	

Another subsample from the plant litters and goose faeces was analysed for the chemical parameters included in the minimum dataset for litter quality composed by Palm and Rowland (1997), namely 'lignin' (more correctly acid-insoluble-carbon as it may contain other recalcitrant carbon-fractions besides true lignin), soluble carbon, soluble phenolics, α-cellulose, total nitrogen, total carbon, total phosphorous and ash-free dry weight. Table 2.1 summarizes the protocols used for analysis of the different parameters and if the parameters are considered important for the short-term decomposition / nutrient release rate or the long-term decomposition / soil organic matter formation.

Before analysis litter was ground using a planetary ball mixer (Retsch, MM200, Germany). Especially for graminoid litter and to a lesser extent for roots not enough material could be collected in some grazed plots to analyse them for all parameters. In that case priority was given to carbon and nitrogen analysis followed by the other parameters in increasing order of mass needed for the analysis.

Decomposition and nitrogen release rates

The litterbag method (Bocock and Gilbert 1957) was utilized for estimating decomposition and nitrogen release rates. Litterbags (6 cm x 6 cm between stitching) were made of polyester gauze (0.3 mm mesh width) and filled with 0.2 g ± 0.002 g air-dried litter or goose faeces. Graminoid litter and roots from ungrazed plots, moss litter from grazed and ungrazed plots and goose faeces were incubated in separate litterbags in both the exclosures and their control plots.

For the six exclosures from the Thiisbukta series an extra set of litterbags was placed in separate subplots (20 cm x 25 cm) of each exclosure to investigate the possibly facilitating effect of goose faeces on the decomposition process. Therefore we added five fresh goose droppings from adult geese, corresponding circa 1.9 g of N m^{-2} (van der Wal and Loonen 1998) to these subplots at the end of the growing season in 2007 (start of incubation) and in 2008. This equals a realistic maximum of goose faeces at our study site (M.L., unpublished data). An overview of the amount of litterbags in every plot can be found in table 2.2.

Table 2.2. Overview of the number of litterbags incubated in the different exclosure types

Exclosure series	Treatment	Grass litter	Grass roots	Moss litter		Faeces
				Grazed	Exclosure	
Thiisbukta	Grazed	1	1	3	3	1
	Exclosure	1	1	3	3	-
	Exclosure subplotwith faeces	1	1	3	3	1
Lake Solvatnet	Grazed	1	1	2	2	1
	Exclosure	1	1	2	2	-
Old	Grazed	1	1	3	3	1
	Exclosure	1	1	3	3	-

Litterbags were incubated in the same plots as where their litter was originating from and the coupled plot at the end of the growing season (1-2 September 2007). Moss litter and roots were incubated in the decomposing moss layer, thus at the moss-soil interface. Grass litter and goose faeces were incubated above the moss layer and held in place with wooden skewers. This way we mimicked the position of the litter under natural circumstances.

Litterbags were collected after two years of incubation (30-31 August 2009). In the laboratory, extraneous litter, soil particles, organisms and roots were carefully removed with forceps. The remaining litter was dried at 70 °C until constant weight and the remaining mass was determined. All samples were ground and a 5-6 mg subsample was used for C/N analysis (CN element analyser NC-2100, Carlo Erba Instruments, Italy).

Data analysis

Statistical analyses were performed using SAS version 9.2 (SAS Institute Inc. 2008) and R version 2.10.1 (R Development Core Team 2009).

Relative abundance of different litter types was calculated as the percentage of the total litter mass in the plot concerned. We compared the total necromass and relative abundance of different litter types paired (corresponding grazed plots and exclosures) with Student's t or Signed Rank test depending on normality (SAS).

We tested for differences in litter quality using a mixed model ANOVA with two fixed and two random factors. Litter type (moss and roots and graminoids if enough data was available) and litter origin (grazed and ungrazed) and their interaction were treated as fixed factors. Exclosure series and replica, which is nested within exclosure series, were treated as random

factors (using the lme function in R). In this way, the problem of pseudoreplication (within-replica and within-exposure series correlations) are explicitly taken into account (Venables and Ripley 2002).

Differences in decomposition and nitrogen release rates between grazed and ungrazed plots were tested for using a four-way mixed ANOVA model. Dead organic matter type (moss, roots, graminoids and faeces) and incubation plot (grazed and ungrazed) were fixed factors, and as above, exclosure series and the nested replica effect were added as random effects to avoid pseudoreplication problems. Data were first analysed without the dead organic matter type 'faeces', because they were absent in most of the ungrazed plots and might induce spurious interactions due to the unbalanced design. However, after finding the interaction dead organic matter type – incubation plot to be non-significant we reintroduced the faeces category.

To test for the hypothesis that decomposition and nitrogen release rates differed depending on the origin of litter, we performed a similar four-way mixed ANOVA with moss litter origin (grazed and ungrazed) and incubation plot (grazed and ungrazed) as fixed factors and replica nested in exclosure series as random factors (lme function in R).

Finally we examined the influence of faeces on decomposition and nitrogen release rates using a mixed three-way ANOVA with litter type (moss, roots and graminoids) and incubation plot (only Thiisbukta series, grazed, ungrazed and ungrazed + faeces) as fixed factors and replica as random factor (lme function in R).

Effects were considered significant at $p \leq 0.05$. For the ANOVA, in case of significant effects, a posteriori comparison of means was performed with Tukey corrections for multiple comparisons.

RESULTS

Relative abundance litter

In the exclosures 1.7 times more necromass was present than in the grazed plots (2863 ± 372 g/m² respectively 1689 ± 149 g/m²; t=-2.53, n=6, p=0.05). Moss litter was by far the most abundant both in grazed plots and exclosures, followed by roots and graminoids (figure 2.2).

However, while the general pattern was the same for grazed plots and exclosures, the percentage of litter originating from graminoids and roots was respectively twice and four times as much in the exclosures compared to the grazed plots (figure 2.2).

All differences in relative abundance between grazed plots and exclosures were statistically significant (table 2.3). In none of the cores *Equisetum* spec. litter was found and only one sample, originating from one of the exclosures, contained a small amount of litter from dicotyledons.

Table 2.3. Results of pair wise comparisons of relative litter abundance between grazed plots and exclosures (n=6). Significant differences (p<0.05) are in bold.

Litter type	Test parameter	p
Graminoids	S = 10.5	0.0313
Moss	t = -5.15	0.0036
Roots	t= 5.46	0.0028

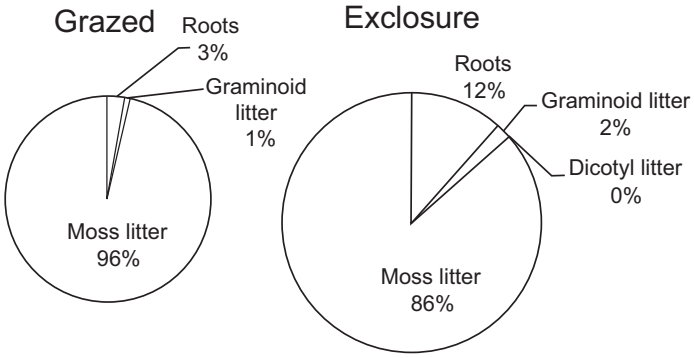

Figure 2.2 Mean relative abundance of different litter types in grazed plots and exclosures from the Thiisbukta series at the end of the growing season (n=6). Total necromass 2863±372 g/m² and 1689±149 g/m² for exclosures respectively grazed plots.

Litter Quality

We observed differences for all measured chemical parameters between litter types, e.g. moss, roots and graminoidsb (table 2.4 and table 2.5). Roots had the lowest concentration of structural compounds ('lignin' and α-cellulose) and the highest concentration of phosphorous, soluble carbohydrates, carbon and ash-free dry mass. For soluble phenolics content, roots showed an intermediate value. Nitrogen content did not differ between roots and graminoid litter or moss litter. Moss litter had the highest 'lignin' content (actually acid-insoluble carbon as mosses do not contain true lignin (Bland et al. 1968, Reddy 1984)) and lowest concentration of nitrogen, phosphorous, carbon, soluble phenolics, soluble carbohydrates and ash-free dry mass. The α-cellulose content of moss litter was intermediate between graminoid litter and roots. Graminoid litter had a higher concentration of α-cellulose, soluble phenolics and nitrogen, for all other parameters graminoid litter showed intermediate values.

Table 2.4. Initial chemical characteristics of litter types (means ± 1 SE). All values are expressed as % of dry weight. Different capitals indicate significant differences between treatments (grazed – exclosure) and different lower case letters indicate differences between litter types ($p \leq 0.05$).

Litter type	'lignin'	Soluble Carbohydrates	Soluble Phenolics	α-Cellulose	Total Nitrogen	Total Carbon	Total Phosphorus	Ash-free dry weight
Grazed	A	A	A	A	A	A	A	A
Roots	5.3 ± 0.9b	34.6 ± 4.9a	0.65 ± 0.05a	16.5 ± 0.6b	1.40 ± 0.14ab	43.0 ± 0.9a	0.206 ± 0.026a	0.839 ± 0.131a
Graminoids	na	na	na	na	1.48 ± 0.19a	42.7 ± 0.9a	0.169 ± 0.071b	na
Moss	13.0 ± 0.8a	2.9 ± 0.4b	0.22 ± 0.017b	22.2 ± 1.3a	1.19 ± 0.07b	34.6 ± 1.4b	0.119 ± 0.007b	0.778 ± 0.030b
Faeces	5.9 ± (*)	2.3 ± (*)	1.16 ± (*)	19.2 ± (*)	2.00 ± (*)	39.8 ± (*)	0.404 ± (*)	0.832 ± (*)
Exclosure	B	A	A	B	B	A	B	A
Roots	3.4 ± 0.5b	35.4 ± 3.1a	0.65 ± 0.03b	16.0 ± 0.9c	1.20 ± 0.08ab	44.5 ± 0.2a	0.146 ± 0.018a	0.968 ± 0.002a
Graminoids	4.2 ± 0.3b	6.1 ± 0.8b	1.07 ± 0.05a	25.1 ± 0.7a	1.35 ± 0.05a	44.1 ± 0.2a	0.127 ± 0.010b	0.923 ± 0.010a
Moss	12.6 ± 0.9a	2.7 ± 0.3b	0.24 ± 0.03c	20.7 ± 1.1b	1.10 ± 0.05b	33.6 ± 1.5b	0.112 ± 0.006b	0.777 ± 0.025b

(*) Pooled samples

Besides those differences in litter quality between litter types, differences between litter produced in grazed plots and exclosures were found (table 2.4 and table 2.5). Litter produced in exclosures exhibited lower amounts of 'lignin', α-cellulose, nitrogen and phosphorous than in ungrazed plots (between 3 – 35 % reduction, with for all parameters but α-cellulose lowest differences for moss litter).

Goose droppings showed intermediate values for structural compounds, higher values for nitrogen, phosphorous and soluble phenolics and lower values for soluble carbohydrates, carbon (except moss from exclosures) and ash-free dry mass (table 2.4).

Differences in 'lignin', carbon, nitrogen and phosphorous content resulted in differences in the most commonly used ratios, C:N, C:P, 'lignin':N and 'lignin':P (table 2.5, figure 2.3) between litter types (all parameters) and between litter produced in grazed plots and exclosures (only C:N and 'lignin':N). Faeces had the lowest values for all quality parameters, suggesting they decompose relatively easy.

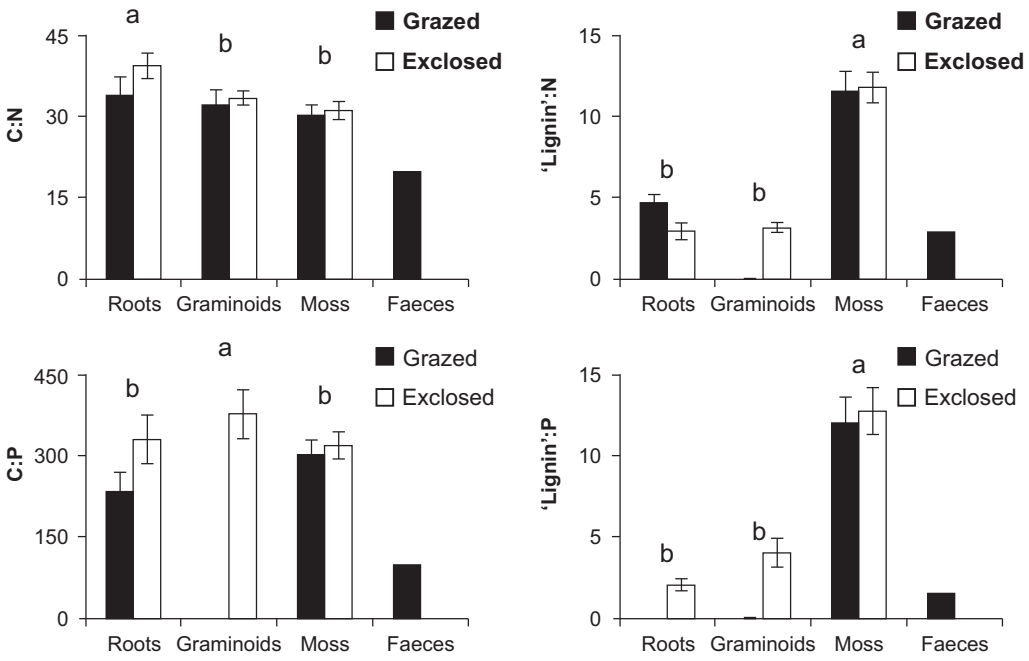

Figure 2.3. Selection of most commonly used ratios of chemical parameters to describe dead organic matter quality (C:N, 'lignin':N, C:P, 'lignin':P) for different litter types produced in grazed plots and exclosures. Error bars indicate ± 1 SE. Different letters indicate differences between litter types, differences between treatments are indicated by a putting them in bold ($p \leq 0.05$).

Table 2.5. Results from the four-way ANOVA's for the different litter quality parameters. Fixed variables were litter type (moss, roots and shoots, or only moss and roots if indicated by *) and treatment (grazed, exclosure), random variables were replica nested in exclosure series. Significant differences ($p \leq 0.05$) are in bold.

Litter quality parameter	Litter type			Treatment			Litter type x Treatment		
	df	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
'Lignin'	2, 45	108.32	**<0.0001**	1, 33	23.91	**<0.0001***	1, 32	0.09	0.7697*
Soluble Carbohydrates	2, 58	114.24	**<0.0001**	1, 42	1.11	0.2986*	1, 41	0.05	0.8321*
Soluble Phenolics	2, 58	210.94	**<0.0001**	1, 42	0.65	0.4249*	1, 41	0.14	0.7092*
α-Cellulose	2, 45	20.59	**<0.0001**	1, 33	5.69	**0.0230***	1, 32	0.12	0.7358*
Total Nitrogen	2, 67	7.08	**0.0016**	1, 67	4.28	**0.0424**	2, 65	0.35	0.706
Total Carbon	2, 67	82.74	**<0.0001**	1, 67	3.64	0.0607	2, 65	1.08	0.3447
Total Phosphorus	2, 35	13.90	**<0.0001**	1,35	5.05	**0.031**	2, 33	2.21	0.1258
Ash-free mass	2, 21	18.08	**<0.0001**	1, 18	0.00	0.9558*	1, 17	1.01	0.3282*
C:N	2, 67	5.98	**0.0041**	1, 67	4.45	**0.0386**	2, 65	0.87	0.4255
'lignin':N	2, 45	69.91	**<0.0001**	1, 33	11.05	**0.0022***	1, 32	0.08	0.7842*
C:P	2, 34	8.56	**0.001**	1, 34	1.51	0.2269	1, 32	2.09	0.1397
'lignin':P	2, 25	30.64	**<0.0001**	1, 17	1.68	0.212*	1, 16	0.01	0.9379*

Decomposition rates

After two years on average between 17% (moss grazed, exclosure) and 54% (roots, grazed) of the litter was broken down (figure 2.4.A).

Decomposition rates were significantly increased by excluding geese ($F_{1,104}$=4.456, p=0.0372) and by dead organic matter type ($F_{3,123}$=30.53, p<0.0001). Whereas all dead organic matter types – graminoids, roots, moss, faeces – differed from each other in decomposition rates except moss litter and faeces (figure 2.4.A), no interaction effect of goose grazing and dead organic matter type on decomposition rates could be observed ($F_{1,102}$=0.1606, p=0.8519). Goose grazing impact on decomposition was thus not significant different between dead organic matter types.

No support was found for the facilitation of litter decomposition in the plot of origin. More detailed analysis of the decomposition rates of moss litter revealed that the breakdown of moss litter was not significantly influenced by the origin of the litter ($F_{1,46}$= 1.689, p=0.2002, figure 2.4.A). Also no evidence was found for a change in decomposition rates when goose faeces were added to the exclosures ($F_{2,61}$=2.126, p=0.1281, table 2.6).

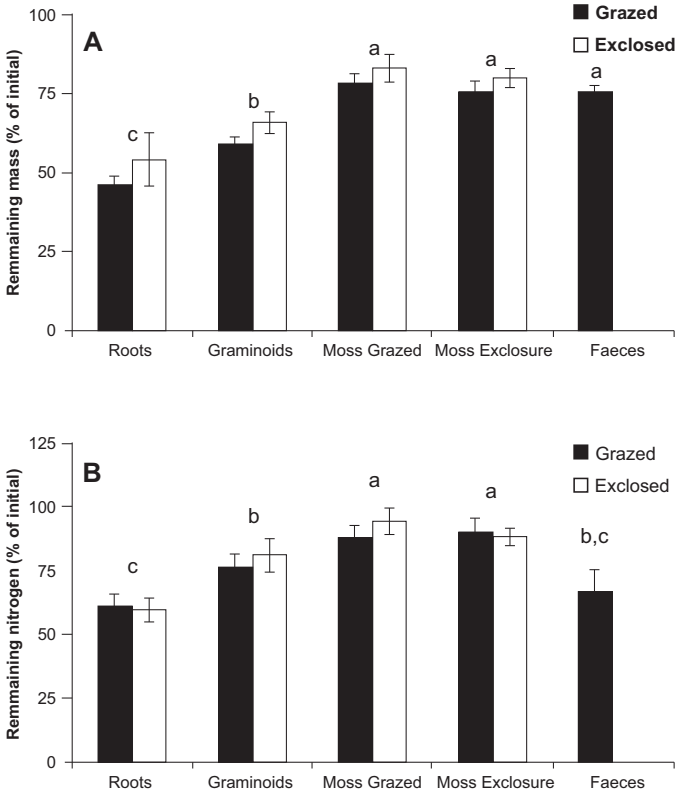

Figure 2.4. Remaining litter mass (A) and nitrogen (B) for different litter types in grazed plots and exclosures. Error bars indicate ± 1 SE. Different letters indicate significant differences between litter types, difference between treatments are indicated by putting them in bold ($p \leq 0.05$).

Table 2.6. Decomposition and nitrogen release from litter in the Thiisbukta plots. Values are given as means ± 1 SE.

Plot type	Litter type	Remaining Mass (% of initial)	Remaining Nitrogen (% of initial)
Grazed	Roots	48.3 ± 4.0	60.5 ± 8.0
	Graminoids	61.3 ± 1.9	88.5 ± 8.8
	Moss Grazed	87.7 ± 4.7	99.6 ± 7.0
	Moss Exclosure	84.8 ± 5.5	97.0 ± 12.0
	Faeces	76.0 ± 7.8	86.7 ± 16.8
Exclosure + Faeces	Roots	52.4 ± 6.8	63.4 ± 12.0
	Graminoids	70.2 ± 8.7	101.2 ± 13.3
	Moss Grazed	94.3 ± 3.4	101.0 ± 7.1
	Moss Exclosure	96.7 ± 2.8	100.5 ± 2.1
	Faeces	79.1 ± 9.6	89.5 ± 13.0
Exclosure	Roots	67.0 ± 20.9	58.3 ± 9.4
	Graminoids	70.3 ± 6.3	93.4 ± 11.2
	Moss Grazed	100.7 ± 5.5	112.6 ± 10.0
	Moss Exclosure	89.0 ± 3.5	96.3 ± 6.5

Nitrogen release

Although at first glance the patterns for nitrogen release might seem rather similar to the patterns for mass loss, they differ on quite essential parts. After two years between 6% (grazed moss, exclosure) and 40% (roots, exclosure) of the nitrogen was released from the litter (figure 2.4.B). Rates of nitrogen release were only significantly influenced by dead organic matter type ($F_{3,123}$=21.37, p<0.0001) and not by goose grazing ($F_{1,104}$=0.21969, p=0.6403) or the interaction between both ($F_{1,102}$=0.2229, p=0.8006). Dead organic matter types which differed significantly in nitrogen release rates were moss and faeces, moss and roots and graminoids and roots. Just as for mass loss no support was found for the facilitation of nitrogen release in the plot of origin; rates of nitrogen release from moss litter were not significantly influenced by the origin of the litter ($F_{1,46}$= 0.2291, p=0.6344, figure 2.4.B). Finally, also similar to mass loss no evidence could be found for a change in nitrogen release rates when goose faeces were added to the exclosures ($F_{2,61}$=0.36969, p=0.6925, table 2.6).

DISCUSSION

The goal of this study was to examine the different ways in which goose grazing might affect decomposition processes in the high Arctic. First we focused on the dead organic matter: plant litter and in the case of goose grazing also faeces. We both examined litter quantity and resource quality.

Litter production itself could not be studied but the necromass (graminoids, dicotyledons, *Equisetum* spec. and moss excluding the peaty soil) and total root mass was considered as a proxy for litter production. As decomposition rates varied between litter types the relative production of litter will not be the same as the relative abundance of litter. The use of the total root mass further biases the picture. However, assuming that goose grazing has no (or only a minor) effect on root mortality, the differences in relative abundance of litter between grazed and ungrazed plots will be translated in analogue differences in litter production as the difference in decomposition rates between different litter types was not influenced by goose grazing.

Also while discussing the effect of goose grazing on resource quality we have to be careful. It was indeed not possible for us to separate roots trustfully into biomass and necromass, let

alone that we would be able to distinguish between recently senescenced and old root litter. Visual separation of roots has lots of limitations and especially distinguishing live from dead fine roots is subjective and requires tedious microscopic examination of nearly every fine root segment (Clemensson-Lindell and Persson 1995, Ruess et al. 2006); a reason why a series of chemical methods were developed (Clemensson-Lindel 1994, Ruf and Brunner 2003). It goes without saying that we couldn't adopt these methods as we intended to use the root litter for chemical analysis and to study decomposition. As a result we decided to use total root mass, but we are aware of the problems this might cause for comparing litter quality between roots and other litter types.

Keeping these objections in mind, we found that grazing by geese diminishes the amount of litter present. It might sound evidently because plant parts are removed by geese before they can senescence, however the reduction of litter by herbivory is not a general rule. Ford and Grace (1998) found for example 85% more necromass in grazed plots compared to exclosures, which was explained by the destructive feeding habit of their study species: wild boar and nutria. However, other studies on geese found no difference (Zacheis et al. 2002, Sjögersten et al. 2011) or in line with our research a decreased litter production (Bazely and Jefferies 1986, Zacheis et al. 2001). Also the study conducted by Sjögersten et al. (2011) on the same exclosures earlier in the season found only a tendency of decreased graminoid litter presence and no overall effect as we found in this study. This might be due to seasonal differences, as she collected litter at the peak of the growing season before senescense and we collected litter at the end of the season after senescence.

On top of the overall impact of Barnacle Goose grazing on litter quantity we found a shift in relative abundance of litter types between growth forms. The relative abundance of graminoid litter, dicotyledonous litter and roots was reduced in grazed plots while relatively more moss litter was present. This is reflecting the food selection of Barnacle Geese, which prefer grasses and sedges followed by forbs above mosses (Prop and Vulink 1992, Alsos et al. 1998).

Although a shift in relative litter abundance of different species / growth forms by herbivory is often insinuated based on the results of vegetation surveys or biomass production (Olofsson and Oksanen 2002), we found almost no other study which actually quantified the possible shift. An exception is he study of Persson et al. (2005) who found a significant difference in litter production of different plants caused by herbivory. Shifts in vegetation composition

suggest that herbivores might both favour and deplete their preferred food plants depending on among others habitat characteristics (Semmartin et al. 2004) and grazing intensity (Jefferies et al. 2003).

Actually, as digestion efficiency in geese is poor, geese select for plants high in nutrients and low in structural components as 'lignin' (Mattocks 1971, Owen 1980, Prop and Vulink 1992, Alsos et al. 1998), two main characteristic of high quality litter (Berg and McClaugherty 2008). So as Barnacle Geese prefer grasses above mosses we expected grasses to produce better decomposable litter. Indeed we found grass litter having higher nutrient (nitrogen and phosphorous) and lower 'lignin' concentration than mosses and this not only counts for aboveground graminoid litter, but also for the often neglected roots. In general, main nutrients, as nitrogen and phosphorous, primarily enhance decomposition during the early stage, whereas 'lignin' exerts a dominant negative control over the later stages (Berg and McClaugherty 2008). Therefore, we might conclude that the change in litter composition towards a lower percentage of graminoid litter and roots caused by goose grazing is probably unfavourable both for short-term and for long-term decomposition.

The other dead organic matter quality parameters are all seen as important determinants of the decomposition process, but their role is less clear. For instance mass loss of dead organic matter is, especially in the long term, positively associated with α-cellulose, but is also negatively associated with 'lignin' concentration (Hobbie 1996, Palm and Rowland 1997). Melillo et al. (1989) combined both lignin and holocellulose (α-cellulose plus hemicellulose) in their lignocellulose index (lignin to lignin and cellulose ratio) for estimating plant quality and long-term decomposition trends. Graminoid litter has the highest α-cellulose content followed by moss and then roots. Based on α-cellulose alone we might thus expect moss to have a better quality for long-term decomposition than roots. However, the much higher lignin-like content and low nitrogen values of moss litter might mitigate the small decomposition advantage the higher α-cellulose content provides. The concentration of soluble phenolics on the other hand is considerably higher in the graminoid litter and roots than in the moss litter suggesting reduced rates of nitrogen release but not necessarily carbon mineralization (Palm and Rowland 1997).

Concerning the commonly used ratios to express litter quality, differences of 'lignin':N and 'lignin':P between the litter types were most obvious and indicate mosses as having the worst

quality for decomposition (highest values). In contrast C:N and C:P values indicate a slightly worse quality for roots respectively graminoid litter.

In summary, we might conclude that the shift in relative litter abundance of different growth forms caused by goose grazing indeed results in a shift in litter quality since, in agreement with other studies (e.g. Hobbie 1996, Dorrepaal et al. 2005), we found a difference in litter quality between growth forms. As different litter quality parameters point in different directions, it is less clear which growth form has the most favourable overall litter quality for decomposition. However, we might prudently think about graminoid litter and roots, both with a lower relative abundance due to goose grazing, having a better organic matter quality for decomposition than moss. If so the shift in growth form composition of litter by goose grazing deteriorates litter quality.

As should have become clear above, a difference exists in organic matter quality between roots and graminoid aboveground litter. Though roots were not sorted in growth forms, we might look at them as the below ground part of graminoids as dicotyledonous litter was only found in very small amounts in two exclosures. Given the known impact of herbivore exclusion on the root biomass, both in positive and negative direction (Milchunas and Lauenroth 1993), this difference in organic matter quality between roots and shoots shows, unintentionally, an indication for a barely documented way in which goose grazing might impact on the organic matter quality: namely by altering the resource allocation pattern. However, data on root litter separated from living roots is necessary to understand if and how this potential mechanism plays.

On top of this we found goose grazing impact on the litter quality of the same plant organ within growth forms, 'lignin', α-cellulose, nitrogen and phosphorous content are higher in litter from grazed plots compared to exclosures. The goose-induced increment in 'lignin' concentrations might impede decomposition. 'Lignin' is one of the major determinants of litter quality for decomposition (Meentemeyer 1978). In spite of this, the effect of (vertebrate) herbivory on the 'lignin' content of litter seems to be hardly documented, especially for moss litter and for roots. Nevertheless, at least one other study by Semmartin et al. (2008) also studied the grazing effect on 'lignin' in roots. Contrary to our results they did not find a difference in 'lignin' content but found that plants from a grassland grazed by cattle produced litter with lower 'lignin':N ratios than those from the ungrazed site, which likely

contributed to accelerate the decomposition of their litter (Aber and Melillo 1991, Vivanco and Austin 2006).

Litter nutrient (nitrogen and phosphorous) content on the other hand is enhanced in grazed plots, ameliorating litter quality for decomposition. This pattern reflects the often found elevated nutrient contents of grazed plants (Cargill and Jefferies 1984, Phillips et al. 1999). Several mechanisms have been proposed to explain differences in nitrogen concentrations of plant tissue between grazed and ungrazed areas (Bazely and Jefferies 1985, Sirotnak and Huntly 2000, Zacheis et al. 2002). In Ydenberg and Prins (1981) the enhanced nitrogen concentrations were explained by the consequent sustained regeneration of young protein-rich plant tissues as a result of repeated grazing by Barnacle Geese. However, this may not explain the elevated levels of nutrients in grazed litter. The enhanced nitrogen availability through incorporation of litter (Zacheis et al. 2002) and faeces (Sorensen et al. 2009) into the soil by trampling, in contrary, might be (a part of) the explanation. The conversion of plant material into faeces might be another. The addition of faeces and urine or uric acid alone, without grazing, has indeed been shown to result in increased plant nitrogen concentration in some grazing systems (Bazely and Jefferies 1985, Hik and Jefferies 1990).

In fact, grazing short-circuits the decomposition process by the production of faeces (Bryant et al. 1983). This influences the time of conversion of living plant tissue to dead organic matter and the form of dead organic matter: faeces rather than dead leaves (Maclean 1974). Like other authors (Floate 1970, Bazely and Jefferies 1985), we found much higher concentrations of total nitrogen and phosphorous in faeces compared to plant litter resulting in lower - thus more favourable - values for all commonly used ratios to express litter quality for decomposition (C:N, C:P, 'lignin':N, 'lignin':P).

Moreover, faeces seem to provide a readily accessible form of nitrogen (Floate 1970, Bazely and Jefferies 1985). Furthermore, Floate (1970) found that for plant litter large amounts of phosphorous were immobilized, while for faeces only by very low temperatures phosphorous was immobilized. We did not measure the remaining phosphorous, but the rather high loss of nitrogen of goose faeces we found (compared with the main plant material they consisted of, namely mosses, L.F. Personal Observation), supports the theory that goose grazing enhances the plant availability of nitrogen through the production of faeces (Bazely and Jefferies 1985).

Analogous to the fast nitrogen release rates we might expect rather high decomposition rates for goose faeces even more as all commonly used ratios to predict decomposability (i.e. C:N,

C:P, 'lignin':N and 'lignin':P) were favourable. Yet, goose faeces were together with mosses the slowest to decompose. Actually, mosses confirmed their status of being slow to decompose and to release nitrogen (Hobbie 1996, Cornelissen et al. 2007). Unfortunately we were not able to collect enough dicotyledonous litter, but litter decomposition research in cold biomes by Cornelissen et al. (2007) consistently found forb litter to decompose even faster than graminoid litter.

The reduced relative abundance of roots, dicotyledons and graminoids through goose grazing thus impedes both mass loss and nitrogen release from litter while the latest is on the other hand accelerated by the transformation of plant biomass in faeces.

In this study no indication was found for a difference in decomposition or nitrogen release rate between litter from the same type produced in a grazed plot or an exclosure. However, as we were not able to collect enough root or graminoid litter in the grazed plots this part of the study was only performed with moss litter which chemistry was least influenced by goose grazing. In other words, the importance of the effect of goose grazing on litter quality within species for decomposition might be more important than our results suggest.

Even a small difference in litter quality caused by goose grazing and the linked decomposability in Arctic ecosystems can play a pivotal role in determining the amount and quality of organic matter that accumulates in soil because small differences in decomposability at the surface can produce large differences in the proportion of litter that is transferred to depths, where decomposition is lowered by cold and wet conditions (Jones and Gore 1978, Heal et al. 1981).

Measured differences in decomposition rates were not only the result of the differences in litter quality. Indeed also the place of litter production and thus decomposition was mimicked in our experiment. Therefore, root and moss litter experienced the same colder and wetter decomposition conditions prevailing at the moss-soil interface, compared to the conditions at the surface where grass litter decomposes.

The differences in mass loss rates between grazed and ungrazed plots are then again a result of the impact of goose grazing on the conditions for decomposition. The decomposition process is indeed very sensitive for environmental conditions like soil temperature, moisture, nutrient availability and the decomposer community (Swift et al. 1979, Hobbie 1996, Ayres et al. 2009, Liu et al. 2010) and on all of them herbivory was found to have an impact.

Barnacle Geese reduced thickness of the moss layer (paper 1) by trampling and consumption. As moss is a good isolator a reduction in the moss layer results in higher soil temperatures (van der Wal and Brooker 2004, Gornall et al. 2007), which in turn is found to enhance the decomposition process (Hobbie 1996). On top of this a deep moss layer retains water within its structure and reduces evaporation from the soil surface, resulting in wetter soils. A considerable amount of the plots was inundated in spring and the other plots were at least soaked by melt water. Exceptionally high (or low) soil moisture contents may limit decomposition rates (Flanagan and Veum 1974); a reduction in soil moisture content in grazed plots will thus enhance decomposition rates.

The possible increase in soil temperature and decrease in soil moisture by the reduction in moss layer depth can only explain the accelerated litter decomposition of moss litter and roots as those litter types were incubated at the moss-soil interface. We thus should think of other mechanisms to explain the increased decomposition rate of graminoid litter incubated above the moss layer by goose grazing. It might be the production of faeces, wherein nitrogen is present in a soluble form (Bazely and Jefferies 1985). However we did not find an indication of facilitated litter decomposition by the addition of faeces. Also the reduction and incorporation in the soil by trampling, which was reported to increase nitrogen mineralization by Zacheis et al. (2002), is excluded as explaining mechanism since we used litterbags. Changed decomposition rates might be explained by the observed shift in microbial community structure (paper 1), but we do not have any evidence for this. Sure is that we didn't find any indication which points towards a "home field advantage", decomposition facilitation of the litter produced in the same plot, as observed in the reindeer study of Olofsson and Oksanen (2002).

CONCLUSION

In this study we found Barnacle Geese influencing decomposition rates in several ways. They altered the plant species composition, changed the plant chemistry within functional groups and produced faeces. The result is a change in dead organic matter entering the decomposition process.

This resulted on one hand in a decrease of the decomposition process and nitrogen release rates caused by the suppression of graminoid litter production by goose grazing. The goose-induced changes in the decomposition environment, on the other hand, positively impacted on the decomposition. The production of goose faeces finally was, surprisingly, not enhancing the process.

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